LATE SEASON FOOD LEVEL, CANNIBALISM, AND OVIPOSITION IN ADULT MANTIDS (ORTHOPTERA: MANTIDAE): SOURCES OF VARIABILITY IN A FIELD EXPERIMENT

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Abstract.—Feeding experiments in the field with mantids typically have yielded results in which statistical variation could not be attributed to variability in performance of specific individuals. Adult female *Tenodera aridifolia sinensis* Saussure, which were individually marked and confined to replicated enclosures in the field, were subjected to two feeding levels and starvation control. All groups lost weight during the two week experiment; however, this loss was from oviposition in well-fed mantids, from decline in body mass among those which starved. Amount of cannibalism was unrelated to feeding level; however, only cannibals managed to gain body mass in starved and low food level groups. More and slightly heavier oothecae were produced in the high food level group than in the other two; however, cannibals oviposited fewer oothecae than non-cannibals. Variability in performance of individuals within and between treatment groups apparently depended on nutritional history prior to this study as well as to experimental feeding level herein.

Key Words: Mantodea, Mantidae, *Tenodera,* food limitation, cannibalism, predator fitness, predators, experimental variability

Adult female *Tenodera aridifolia sinensis* Saussure (Mantodea: Mantidae) in the northeastern United States must cope with a diminishing food supply late in the growing season, during oogenesis (Eisenberg et al. 1981). Food limitation at this critical time of the season can reduce fitness by decreasing body mass, which in turn decreases the energy available for egg production. The extent of food limitation varies among habitats and years, and it can be alleviated if the mantid fortuitously is perched upon an inflorescence which attracts flower foragers (Hurd 1989).

Although the results of the two studies cited above support conclusions therein,

there was considerable variability in gain or loss of body mass within these field-collected experimental cohorts. The sources for this variability could not readily be ascertained at the time of these experiments because individual mantids were not followed over time. Further, since both of these studies were open field experiments, actual levels of prey availability could not be determined: field-collected groups were compared to cohorts fed *ad libitum* in the laboratory. Since mantids can feed at a rate well beyond the level which produces further gains in body mass (Hurd 1991), it is probable that the numbers of prey consumed by these laboratory cohorts were greater than would translate into enhanced fitness. Thus we cannot infer that mantids from the field

which gained body mass at the same rate as those fed *ad libitum* in the laboratory necessarily ate the same number of prey. It is also possible that some mantids which gained biomass in the field resorted to cannibalism in the absence of alternate prey. In the laboratory well-fed mantid nymphs rarely ate each other, whereas starved nymphs exhibited cannibalism rates in excess of 20% (Hurd and Eisenberg 1984). Therefore it is possible that the tendency toward cannibalism in adults is related to hunger level.

The present study was designed to relate food level, body mass, oviposition, and cannibalism in individual adult female *T. a. sinensis* in the field at the end of the growing season. We monitored individual performance for these variables in order to determine the sources of statistical variability which typically have attended experiments with field-collected animals whose early life history is not known.

Materials and Methods

The study site was a pasture on the Experimental Farm of the University of Delaware, Newark, Delaware. There were resident populations of three species of mantids in this field: *T. a. sinensis,* its congener *T. angustipennis* Saussure, and *Mantis religiosa* Linnaeus.

Twelve 1-m³ enclosures were set up in the field in September 1990. Enclosures were constructed of Lumite Saran netting (12 × 12 strands/cm²) fitted on PVC frames with the bottom side left open to the ground and vegetation within the cage. Cages were stapled to the ground and tightly fitted to 7-cm-high squares of aluminum sheeting which penetrated the soil to a depth of 3–4 cm to prevent migration of arthropods under the mesh. The top of each enclosure was zippered on three sides to allow access. Prior to this experiment each enclosure was emptied of arthropods through a combination of D-Vac suction, pit traps, and hand search. These enclosures allowed us to keep man-

tids under field environmental conditions, and at the same time to control food level and follow individuals during the course of the experiment.

On 24 September, 24 adult female *T. a. sinensis* were collected and weighed. On 25 September these mantids were randomly placed in the enclosures, one pair to each cage. Each enclosure then was randomly assigned to one of three treatment groups (four per treatment) which differed in the number of prey to be added: 1) H = high food level, in which 10 insect prey were added twice weekly, 2) L = low food level, in which five insects were added twice weekly, and 3) Z = zero food level, in which no prey were added. Experimental prey levels were in the range suggested by Bartley (1983). Mantids were color coded with nail polish applied to the dorsal surface of the prothorax, so that individuals could be identified from each pair. Prey were collected from the pasture with a sweep net, and represented the available insect biomass present at that time of year: primarily honey bees with an occasional cricket or grasshopper. Prey were distributed arbitrarily among enclosures according to the above feeding regimes.

Each time food was added, all enclosures first were checked for oothecae, which were removed and weighed. Since more than one ootheca was never found in any cage at the same time, the deflated condition of the abdomen following recent oviposition made it easy to tell which mantid in each pair was responsible. Mantids were weighed at the end of each week, at which time any cannibalism which had occurred was noted. The experiment was terminated on 9 October, since prey were by then too scarce to continue, and the possibility of a killing frost was relatively great.

Results

Mean body mass declined in all three treatment groups from 25 September to 9 October (Table 1). Final mass in treatment Z was 25% lower than initial mass; H and
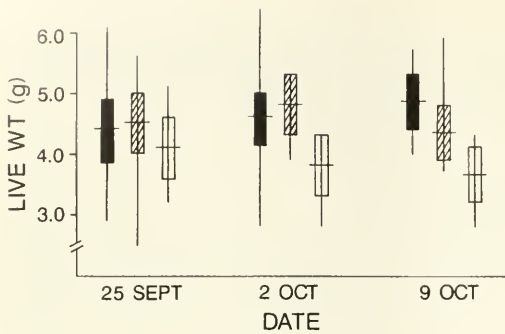
Fig. 1. Change in body mass of adult female *Tenodera aridifolia sinensis* in field enclosures over time. Figures represent range (vertical lines), mean (horizontal lines), and 95% confidence limits (boxes) for LSD ranges. Treatments: Z (unfed) = open boxes; L (low food level) = hatched boxes; H (high food level) = shaded boxes.

L mantids lost 19% and 16%, respectively, over the same period. As a result, there was no significant difference in mean body mass among treatment groups at the end of the experiment. However, since each ootheca produced during the experiment could be attributed to an individual, we could partition out the loss of mass due to oviposition from loss of body mass due to simple starvation. When weights of oothecae were added back to the weights of mantids responsible for them, the treatment groups diverged over time: starved mantids in treatment Z lost weight, those in H gained, and those in L were intermediate (Fig. 1). By the end of the experiment these differences were statistically significant ($F_{2,14} = 4.53$, $P = 0.03$).

There were two cannibals in both treatments H and Z, and three in L (Table 1). Therefore the tendency toward cannibalism was not related to food level. However, non-cannibals lost an average of approximately 18% of initial body mass (exclusive of oviposition loss) in treatment Z over the two weeks, 16% in L; cannibals gained <1% in Z and 4% in L. Both cannibals and non-cannibals gained mass in treatment H: 18% and 10%, respectively.

During both weeks of the experiment, all individuals in Z lost body mass except the two cannibals, numbers 1a and 7b (see "% change," Table 1). Treatment L produced mixed results in this regard: only two individuals, a cannibal (2b) and a non-cannibal (3a), gained weight during the first week, and one cannibal (11a) lost weight. During the second week 11a gained weight, but cannibal 4a lost. There were no cannibals during the first week in H, and half the individuals gained body mass. Cannibals 6a and 10b made substantial gains the second week, while non-cannibal 8b was the only other individual to gain.

Mantids in all three treatments oviposited, but no female produced more than one ootheca (Table 1). Five oothecae were found in H, and three each in L and Z. Among mantids which survived until the end of the experiment, only one failed to oviposit in treatment H, and three each in L and Z. There was no obvious tendency for any treatment group to oviposit earlier or later than the others. Ootheca mass was not statistically different among treatment groups, although the two heaviest were found in treatment H. Cannibals did not generally produced larger oothecae than non-cannibals, and in fact produced fewer oothecae than non-cannibals in all three treatment groups.

DISCUSSION

A comparison of Fig. 1 with Table 1 suggests that although the decline in weight among mantids in treatment Z was due mainly to loss of body mass through starvation, weight decline in well fed mantids could be attributed primarily to oviposition. The fact that treatments could not be differentiated simply on the basis of changes in raw mantid weights means that it would be difficult to assess the food quality of a habitat simply by sampling individuals at different times while oviposition is occurring. Such comparisons would be valid only prior to the onset of oviposition, as in Eisenberg et al. (1981) and Hurd (1989).

In any case, oviposition was an important

Table 1. Live weights (g) of adult female *T. a. sinensis*, and weights of oothecae in experimental enclosures at three different food levels. "% change" denotes the percentage of weight change between consecutive sample dates which was not accounted for by oviposition: weight of ootheca was added to subsequent body weight, this sum subtracted was from previous body weight, then the difference was divided by that previous weight ($\times 100\%$). Ootheca weights are positioned to indicate time interval during which oviposition occurred. "Mantid no." denotes randomly assigned enclosure number and individual (a or b) of each pair assigned to each enclosure. C = death by cannibalism since last sample date.

Food	Mantid no.	25 Sept	Ootheca	2 Oct	% change	Ootheca	9 Oct	% change
High	6a	5.72	1.60	3.40	−12.6		4.10	+20.6
	6b	4.30		4.40	+2.3		C	
	8a	6.09		6.40	+5.1	1.75	3.61	−16.3
	8b	3.50		4.50	+28.6		4.85	+7.8
	9a	3.67	1.72	4.10	+58.6		2.55	−37.8
	9b	5.31		5.30	−0.2	1.37	3.61	−6.0
	10a	3.67		3.50	−4.6		C	
	10b	2.91		2.80	−3.8	1.27	2.70	+41.8
Mean (SE) =		4.40 (0.41)		4.30 (1.15)			3.57 (0.86)	
Low	2a	2.54		C				
	2b	3.03		3.90	+28.7		3.73	−4.4
	3a	4.79		5.00	+4.4		4.15	−17.0
	3b	4.82		4.80	−0.4	1.27	2.66	−18.1
	4a	5.04		4.60	−8.7	1.61	2.45	−11.7
	4b	5.57	1.27	4.00	−5.4		C	
	11a	5.41		5.20	−3.9		5.88	+13.1
	11b	4.80		C				
Mean (SE) =		4.48 (0.38)		4.58 (0.53)			3.77 (1.38)	
Zero	1a	4.25		4.00	−5.9	1.29	3.04	+8.3
	1b	4.01		3.80	−5.2		C	
	5a	5.11		4.30	−15.8	1.20	2.82	−6.5
	5b	4.11		3.90	−5.1		3.56	−8.7
	7a	3.56		C				
	7b	3.24		3.70	+14.2		3.20	−13.5
	12a	5.09	1.41	2.80	−17.3		2.58	−7.9
	12b	3.34		2.80	−16.2		2.80	0
Mean (SE) =		4.09 (0.25)		3.61 (0.59)			3.00 (0.35)	
F =		0.35		2.35			1.07	
df =		2, 21		2, 18			2, 14	
P =		0.71		0.12			0.37	

source of variability in our experiment. Some females oviposited earlier in the experiment, which could result from differing stages of development and oogenesis among an asynchronously hatching cohort (Hurd 1988, Hurd and Eisenberg 1989a, b). Some produced larger othecae, reflecting more eggs (Eisenberg and Hurd 1977). The fact that initial weights of females used in this experiment ranged from 2.5 to 6.1 g indicates that these mantids had quite different nutritional histories despite having been collected from the same field at the same time. Thus the variability in egg production was a function of variability in feeding condition earlier during the life cycle. This in turn was undoubtedly a function of within-habitat heterogeneity in the availability of prey, produced for instance by patches of flowers (Hurd 1989).

Surprisingly, cannibalism was neither related to food level nor generally beneficial in terms of egg production for mantids in this experiment. However, judging from live weight data, it did contribute significantly to the diets in treatments L and Z: cannibals in these groups were the only individuals to exhibit substantial gains in body mass both weeks of the study. This was also true of treatment H during the second week, but not during the first when there was no cannibalism. The potential benefit of cannibalism to starved mantids in treatment Z is clearly a direct contribution of biomass by the victim; in the fed groups, cannibalism also could have alleviated competition for alternate prey (Hurd and Eisenberg 1990b). In fact, a cannibal such as 2b (Table 1) from treatment L effectively doubled its available prey, elevating its food level to that of an individual in one of the pairs in treatment H. This is therefore another source of variability in the data, which may reflect an advantage of cannibalism for these mantids in nature at the end of the growing season by reducing competition for increasingly limited prey. Since oothecae of *T. a. sinensis* are spatially aggregated (Eisenberg and Hurd 1990), it seems likely that adult females encounter each other in nature at this time.

The change in body mass other than from oviposition (% change, Table 1) was generally more variable among fed mantids in treatments L and H than in Z, even between members of a pair in the same enclosure. Although in Z the only food was the other member of the pair of mantids, food provided to H and L enclosures probably was not evenly divided between the occupants thereof. For instance, 9a in treatment H was able to produce the second largest ootheca in the experiment as well as to gain body mass during the first week, while 9b did not oviposit and lost body mass. Thus differences in actual feeding rates within, as well as between, cages likely was another important source of variability in this experiment. Uneven apportionment of resources among individuals in nature undoubtedly is the rule. Therefore, although the average of approximately 3 bees provided/mantid/day was sufficient to alleviate food limitation in treatment H relative to the other treatments, an individual of any pair may actually have eaten 0–6 bees/day. Even among individually caged mantids kept under identical conditions in the laboratory, feeding rates can be quite variable (Hurd and Rathet 1986).

The remaining variation in performance among individuals in this experiment could have been a function of activity level; i.e. even among unfed, non-cannibalistic mantids in treatment Z where actual feeding rates were all zero, some individuals may have lost more body mass than others because their activity levels and consequent energetic demands were higher. This may have been most important in the starved cohort, since food limitation can induce dispersal behavior in these mantids, at least as juveniles (Hurd and Eisenberg 1984).

All of these sources of variability not only reflect differences in response to environmental conditions by individual mantids, but they also may be responsible for variation in impact on the prey community. This could be exhibited in the amount of direct reduction of prey, or even in the direction of impact. These predators are capable of indirect effects such as enhancing survivorship of one prey species by interfering with the impact of other predators on that prey species (Hurd and Eisenberg 1990a).

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